Grapevine adaptations to water stress: new perspectives about soil/plant interactions

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Title:

Grapevine adaptations to water stress: new perspectives about soil/plant interactions.

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Abstract

Grapevine adaptations to water-stress are described, by focusing on soil/root interactions and root-to-shoot signaling to control both plant water relations and fruit ripening process. Root response to drought, tolerance of available rootstock germoplasm, mechanisms of embolism formation and repair in root, aquaporin control of plant water relations, and abscisic acid biosynthesis and delivery are highlighted, by reviewing recent insights coming from either (eco)physiological literature or viticultural assays addressing vineyard-soil relationships.

Key-words

Abscisic acid (ABA), aquaporin; isohydric; anisohydric; embolism.

General overview

In viticulture, the knowledge of the right soil water deficit to be applied to the vineyard is a key factor to obtain high quality wines (Costa et al. 2016). Although the role of soil properties and management in wine production is acknowledged as determinant of *terroir* expression (van Leeuwen et al. 2004), the soil component is generally perceived as secondary to climate and canopy management, and its influence on root water uptake is scarcely documented in the viticultural literature. In general, grapevines can be grown on a wide variety of soil types, for which the main intrinsic characteristics to be considered are adequate depth and good internal drainage, texture, pH and salinity. These properties, together with the level of water supply to the soil (natural by rainfall or artificial by irrigation) define the water availability to the plant at the soil-root interface (Passioura 2002).

Another component to influence the soil-plant relationship is the selection of the rootstock genotype (Ollat et al. 2015). Nowadays, in fact, more than 80% of the grapevines grown around the world are phylloxera-susceptible European scions grafted to rootstocks that are usually hybrids of tolerant American species (Whiting 2005). Nevertheless, grafting represents not only a tool for straighten the grapevine tolerance or resistance to root parasites, but also a way to influence scion vigour and crop maturity, or plant tolerance to adverse soil conditions (e.g. drought, water logging, lime, salinity, low pH, low temperatures, etc.) (Keller 2010). Most of grape rootstocks are hybrids of *Vitis berlandieri*, either with the xerophylic species *Vitis rupestris* or with the mesophylic species *Vitis riparia*, being *V. berlandieri* × *V. rupestris* hybrids generally more drought tolerant and vigorous than *V. berlandieri* × *V. riparia* hybrids (Tramontini et al. 2013a, b). In spite of the recognised value of rootstock selection for improving scion's adaptability to specific soil conditions, much of the information available on the drought tolerance of commercially available rootstocks and on differences generated by rootstock/scion combinations has been for long time mainly based on anecdotal evidence or visual comparisons (Soar et al. 2006a). In the recent years, more attention has been devoted to the study of the influence of rootstock genotype to scion gas exchange as a consequence of its intrinsic characteristics (genetic, anatomical and physiological specificities of the root system) and of the metabolic control imposed via hormonal signalling (Soar et al. 2006a, b; Koundouras et al. 2008; Tandonnet et al. 2010; Comas et al. 2010; Alsina et al. 2011; Marguerit et al. 2012; Tramontini et al. 2013b; Berdeja et al. 2015; Ollat et al. 2015).

More in detail, roots absorb and convey most of the water and nutrients required by the aerial parts of the plant and synthesize the hormones needed for an adequate development of the shoot system. The root water uptake capacity contrasts therefore the risk of plant tissues dehydration, consequent to abiotic stresses (Aroca et al. 2012). The root water uptake rate is the result of the combined effect of osmotic and hydrostatic forces: the former due to the root pressure (generated by the active transport of solutes and biosynthesis of new osmolytes) and the latter due to the cohesive pull generated by the leaf transpiration on the whole water column. When the water enters the root system, it moves along axial and radial ways, throughout the xylem vessels in the first case and via apoplastic and cell-to-cell path in the second case. Both ways bring certain resistances to the flow: cavitation of the xylem vessels, drop in water potential during water displacement through the pores between the fibrils of the cell wall and through the intercellular spaces (apoplast path), along the network of cell cytoplasm interconnected by plasmodesmata (symplast path), across the cell membranes (transmembrane path) (Steudle and Peterson 1998; Aroca et al. 2012). According to Ohm's law analogy, commonly applied to plants, these resistances are additive (Tyree 1997). They modulate the water flow produced by gradients in osmotic pressure and water potential, which respectively control the two parallel and interacting cell-to-cell and apoplast pathways. Between the two paths, the cell-to-cell is considered predominant under limited transpiration conditions, while the apoplast under well-transpiring conditions (Steudle 2000; Javot and Maurel 2002). The two pathways require some more in-depth analysis for their interconnection with the aquaporin activity and cavitation events, which are in turn related (Kaldenhoff et al. 2008; Tramontini and Lovisolo 2015).

A last aspect to be mentioned concerning the soil-root interaction is the root-to-shoot hormonal signalling, in particular the synthesis and transport of abscisic acid (ABA). When the soil water potential declines, ABA acts as a messenger indicating water stress from the roots, via the xylem sap, to the guard cells in the leaves and inducing the stomata closure (Hartung et al. 2002). When the water availability is recovered to an adequate level, the roots stop releasing the hormone and the stomata re-open. The delayed interruption of the signal, much more gradual than the initial release, suggests a further role of the hormone on the embolisms repair (Lovisolo et al. 2008a). The relative importance of the chemical signalling compared to the hydraulic balance in the plant response to water stress remains a debated issue (Chaves et al. 2010; Tombesi et al. 2015) also investigated through numerical models (Huber et al. 2014, 2015).

As a further detail, soil water unbalance affects berry quality by modifying accumulation of secondary metabolites. The role of ABA is a pivotal link between berry ripening process and grapevine response to stress. The response to abiotic stress at the berry level drives the accumulation in berry pulps, seeds and skins of secondary metabolites as a line of defense against cell damages. According to soil and vintage, viticultural practices can be managed to control stress plant response in order to influence berry secondary metabolite concentrations and profiles, reflecting on an enhancement of berry quality and on grape and wine nutraceutical and health benefits (Ferrandino and Lovisolo 2014).

Aims

The need for a better understanding of the hydraulic physiological dynamics of crops upon water scarcity is globally acknowledged, as the optimization of the water resources has finally become a priority in the perspective of a sustainable agriculture (Marris 2008). Grapevine is an ideal study plant, due to its intrinsic physiological characteristics (perennial, adapted to arid and semi-arid conditions) (Lovisolo et al. 2010), and the importance of its most renowned final product, the wine (Goode 2012). The latter has driven the grapevine to a worldwide distribution, under very diverse growing conditions, together with the awareness for the added value of the *terroir* component and the complexity of the mechanisms involved in the definition of its qualitative attributes, especially related to vineyard soils. In addition to that, the optimal conditions for growing grapevine plants devoted to the production of world class wines are those of moderate water stress, where the adequate plant sink–source balance is modulated to limiting climate and soil traits (Chaves et al. 2007; Medrano et al. 2015).

Vineyard soil water status

Soil water availability to plants, or soil water-holding capacity, is expressed as % or as mm of water/cm of soil, and depends mainly on soil texture, organic matter content, coarse element content (gravels and rocks) and depth. Pore size varies greatly among textural soil categories and contributes to soil matrix potential (Ψ_M). The lower the pore size the lower the Ψ_M, and therefore the lower the soil water potential (Ψ_{soil}) and water availability to plants.

This effect of texture is however time-dependent. For instance, just after a rain event, sandy soils will have a higher water holding capacity as compared to clayey soils that are characterized by numerous small size pores (< 2μm) and lower soil Ψ_M. In clay soils, small pores apply capillary forces to water and, together with the important electrostatic interactions between clay particles and water molecules, trap the fluid inside the empty

spaces. For the same reason, a coarse-textured or sandy soil will dry more rapidly than a fine-textured soil, limiting the water availability to plant over time and forcing its roots growth toward deeper levels. The soil organic matter influences the soil aggregation and associated pore space distribution, and is comparable to clay in terms of its effect on water holding capacity (Saxton and Rawls 2006). Deep soils will contain more water than shallow soils and will dry more slowly, unless they present a coarse texture: in this case, as already mentioned, due to the high drainage, the plant will develop deeper roots (van Leeuwen et al. 2004). Soil water holding capacity varies from < 100 mm/cm in shallow gravelly soils to > 300 mm/cm in deep loamy soils. Overall, water stress is favored in shallow coarse-textured soils. In a vineyard, severe water stress is characterized by very low soil water potential ($\Psi_{soil} \leq -0.8$), moderate water stress corresponds to $-0.3 > \Psi_{soil} > -0.6$ and light water stress to $\Psi_{soil} \geq -0.3$ (Ojeda 2008).

Grapevine root water status

In conditions of high soil water availability, the grapevine water status is in phase with the air and the soil water status; in the course of the day, for instance, when the air water potential drops, due to evapotranspiration the vine water potential drops as well, in parallel with drops in soil water potential. However, in drought conditions, the grapevine modifies its conductance to water through several mechanisms, that vary among *Vitis* species and cultivars, with consequences on its water status and, finally, on its performance.

In grapevine root, water absorption occurs radially via cellular (symplastic and transmembrane) and apoplastic (between cells) pathways, mainly at the level of unsuberized, meristematic portions of root tips, where the water conductivity per unit of surface area is particularly high. This condition is essentially guaranteed by the high expression and activity of aquaporins in cells (transmembrane pathway) along the axial path of absorption. In secondary growth zones of root tips, which are suberized, the hydraulic conductance is more than 10 times lower than in meristematic and elongation zones, with lower expression of aquaporins (100- to 1,000 times less aquaporin isogenes expressed), but the contribution to water absorption is compensated by the vast proportion of secondary growth zone on the total root system surface area (Gambetta et al. 2013).

The flow of water through the apoplastic pathway toward the xylem conduits mainly relies on water potential differences between the soil and the root. Water flow resistances in the apoplastic pathway are mainly suberized barriers including the Casparian band and the

suberin lamella in maturation and secondary growth portions of roots. These barriers are solute impermeable but their impedance to water flow is not established. The water flowing through the transmembrane pathway faces a resistance intrinsic to the plasma membrane properties, which mainly depends on aquaporin expression and activity. Aquaporin activity is regulated at the post-transcriptional level through phosphorylation, glycosylation and by intracellular pH (Galmes et al. 2007). Various aquaporin isogenes are expressed in the grapevine root tips (Baiges et al. 2001; Gambetta et al. 2013) with some showing a level of specificity for the roots compared to other organs (Shelden et al. 2007, 2009). The aquaporin contribution to hydraulic conductance of roots ranges from 4 to 40%, as shown by experiments performed using aquaporin inhibitors (Lovisolo et al. 2008b; Gambetta et al. 2012) and transgenic grapevines overexpressing root aquaporins (Perrone et al. 2012a).

Root system development and genotype specificities

The main driver for root development is soil water content (Serra et al. 2014). Soil texture and structure have therefore a major role to play in the root system architecture and depth, regardless of the genotype (Barrios-Masias et al. 2015). However in similar soil types both the scion and the rootstock genotypes were shown to have an impact on root development in grafted vines. Tandonnet and colleagues (2010) have shown that, during the first growth cycle, the scion-effect accounts for 42.5% of variance on root dry weight, while the rootstock effect for 1.5%. On their side, rootstocks can confer more or less vigor to scion (shoot growth rate) and this trait is generally attributed to their ability to tolerate water stress during the growing season. Table 1 lists common rootstocks with their genotypic origins and reported level of “tolerance” to drought. The latter is associated with different root growth behaviors that are regulated interactively by water availability, time of year, age of plant and soil depth (Bavaresco and Lovisolo 2000; Bauerle et al. 2008). For example, the drought tolerant rootstock 1103P (*V. rupestris* × *V. berlandieri*), known to confer high vigour to scion, produces a vast proportion of its root biomass in the months following plantation and during summer time, with increased rate in irrigated soil, and shows growth sensitivity to soil depth. Conversely, the little vigorous rootstock 101-14Mgt (*V. rupestris* × *V. riparia*) grows roots gradually over time after plantation, preferentially in winter, and shows much lower growth plasticity to soil moisture level or depth compared to 1103P. Furthermore, the high hydraulic conductance of 1103P root-system is supported by longer root vessels, higher cross-sectional area of first order roots and larger trunk diameter than 101-14Mgt (Alsina et al. 2011).

The intrinsic capacity of roots to absorb soil-contained water thus mainly relies on

genetically- and environmentally-determined expression of aquaporins and xylem architecture. However extrinsic factors such as root-associated mycorrhizas are also known to contribute to grapevine water dynamics (Schubert and Cravero 1985; Nikolaou et al. 2003; van Rooyen et al. 2004) and should not be underscored as determinants of grapevine response to water stress at the root/soil interface.

Root response to drought: ABA synthesis

Low soil water availability causes osmotic stress in grapevine root cells, which in turn changes their metabolic activity. This implies a decreased activity of the plasma membrane H^+-ATPases that normally pump protons in the apoplast, resulting in an increased extracellular pH that is reflected on the xylem sap pH (Keller 2010). In the meantime, osmotic stress causes the up-regulation of genes involved in ABA synthesis. ABA is a "biochemical signal" belonging to a class of metabolites known as isoprenoids, with the main function of regulating the plant water balance and osmotic stress. It is derived from the oxidative cleavage of xanthophylls, themselves derived from the carotenoid zeaxanthin (Nambara and Marion-Poll 2005). ABA is under protonated form (ABAH) under normal condition in xylem sap whereas it becomes dissociated ($ABA^- + H^+$) in the xylem of water-stressed plant. Cell membranes are impermeable to the dissociated form, ABA^-, which cannot be absorbed by xylem parenchymal and leaf mesophyll cells, and is then redistributed to plant organs. ABA^- acts mainly on the guard cells causing stomatal closure and therefore reducing evapotranspiration. ABA also induces the production of dehydration-tolerance proteins, and antagonizes shoot cell growth by counteracting auxin-induced cell wall loosening as well as cell division (Keller 2010). On the other hand, ABA may have an opposite effect on root cells, by promoting auxin-dependent primary root and hair growth under water stress, as observed in *Arabidopsis thaliana* and *Oryza sativa* by Xu et al. (2013).

In grapevine, the importance of ABA synthesis in roots in response to decreasing Ψ_{soil} was recently shown by Speirs et al. (2013). They reported that the expression of ABA biosynthetic genes *NCED1* and *NCED2* was higher in the roots than in the leaves upon drought and highest in the roots in months when soil moisture declined, vapor pressure deficit (VPD) was at its highest and stomatal conductance was impaired. *NCED* expression in roots was correlated with ABA abundance in the roots, in the xylem sap, and in leaves. In addition, studies where grapevines were submitted to partial root drying (PRD)-irrigation have evidenced that the increase in root:shoot ratio occurring in such context is accompanied by an ABA accumulation in the drying roots (Lovisolo et al. 2002a; Stoll et al. 2000) which tend to grow toward deeper

soil layers compared to wet roots (Dry et al. 2000). The different rootstock behaviors in response to drought described in the previous section could also be attributable to different propensities to synthesize ABA as different concentrations were found in the xylem sap of the same scion grafted over different rootstocks (Soar et al. 2006a). However, the level of ABA in xylem sap may not be the most suitable factor to estimate the propensity of roots to synthesize ABA, as proposed by modelling studies showing that root and leaf water status were better response factors to root ABA accumulation in drying soil compared to xylem ABA concentration (Tardieu 2003).

Evidence for ABA synthesis in shoot

Although wide evidence of ABA root biosynthesis and root-to-shoot ABA message comes from PRD experiments involving split-rooted grapevines (reviewed by Lovisolo et al. 2010 and Chaves et al. 2010), the production of ABA by roots in response to soil water deficit is a controversial issue. In fact, there is recent evidence to date mostly in other plant species pointing either to ABA production in shoot or to different roles of root-sourced ABA.

In this sense, Christmann et al. (2007) produced compelling evidence that osmotic stress applied to arabidopsis, maple and beech roots reveals ABA-dependent reporter gene expressions only in the leaves. They showed that shoot response to limited soil water supply is not affected by the capacity to generate ABA in the root, but that the response requires ABA biosynthesis and signalling in the shoot. Soil water stress elicits a hydraulic response in the shoot (that we can hypothesize embolism-related), which precedes ABA signalling and stomatal closure. Further evidence underlining shoot ABA role under water stress was provided by Holbrook and coworkers (2002), who demonstrated that stomatal regulation depends on the shoot genotype only, by grafting of wild type and ABA-deficient tomatoes. In addition, McAdam and Brodribb (2014) showed in a conifer that the strong correlations between foliar ABA and stomatal conductance observed in whole plants in the field and controlled environmental conditions, as well as in detached stems exposed to water stress, were consistent with the functional pool of ABA solely derived from foliage. Recently, the same authors (McAdam and Brodribb 2015) demonstrated that even the response to air VPD was mediated by rapid *de novo* biosynthesis of ABA in the leaves, with no influence of ABA stored in a pool previously.

In grapevine, Soar et al. (2004) described higher concentrations of leaf ABA towards the apex that correlated negatively with stomatal conductance. To investigate the source of the ABA responsible for these gradients they designed a series of girdling and decapitation

experiments. In those experiments, ABA effects were studied at the level of gene transcript, showing that levels of expression of *VvNCED1* reflected the gradients in leaf ABA concentration and concluding that [ABA] gradients in mature leaves and xylem derived from local synthesis. Importantly, the *in situ* regulation of ABA was further demonstrated by Speirs et al. (2013) who showed that the expression of *Hyd1*, a gene encoding ABA 8-hydroxylase (protein controlling ABA catabolism) was elevated in leaves when VPD was lower than 2.5 kPa and minimal at higher VPD levels. This provided evidence that changes in ABA catabolism near its site of action allows optimization of gas exchange to current environmental conditions.

Localization of ABA synthesis in the plant and ABA actions in the plant compartments are summarized in figure 1.

Root response to drought: embolism formation and recovery

When soil water availability does not suffice atmospheric demand, embolisms occur in the xylem vessels (Knipfer et al. 2015a, b; Tramontini and Lovisolo 2015). This phenomenon is common in grapevine (Lovisolo et al. 2002b, 2008b; Choat et al. 2010) and involves the separation of gas molecules that are dissolved in water under the high tension created by elevated transpiration rates (Brodersen et al. 2013). The gas molecules tend to accumulate together causing a disruption of the water column in the xylem and a decrease in hydraulic conductivity. Embolisms occur more frequently in roots and petioles than in shoots, causing 80%PLC (Percent Loss of hydraulic Conductivity) during a moderate water stress in these anatomical compartments compared to the 50% PLC of shoots (Lovisolo et al. 2008a; Hochberg et al. 2016). Root embolization is thought to limit water use by the plant and be protective against the propagation of low xylem tension to the stem. Its importance over chemical signalling for stomatal regulation have been suggested by modelling studies showing that most transpiration responses to PRD treatments could be interpreted by hydraulic signalling alone, and that regulation of stomatal conductance by chemical transport was unstable and oscillatory (Huber et al. (2014, 2015)).

Once again the grapevine genotype seems to modulate the level of root embolization, and thus root hydraulic conductance, in response to water stress. In well-watered conditions, the diurnal dynamic of root hydraulic conductance is either minimal at midday in a drought-sensitive rootstock (such as *V. riparia* × *V. berlandieri,* 420A in Lovisolo et al. 2008a) or maximal in a drought-tolerant *V. vinifera* cultivar (such as Chardonnay in Vandeleur et al.

2009). A drought-sensitive cultivar such as Grenache shows a lower whole-root-system hydraulic conductivity following a period of drought that is associated with decreased root cell hydraulic conductance and lack of aquaporin transcriptional regulation compared to the tolerant Chardonnay (Vandeleur et al. 2009). Moreover, drought-sensitive cultivars present an increased level of suberization in root tips following water stress episodes, thought to be a protective mechanism against water losses from roots. In the same way, drought-resistant rootstocks (1103P and 110R) have higher fine root hydraulic conductance associated with higher expression of aquaporin isogenes even in well-watered conditions compared to drought-susceptible rootstocks (420A and 101-14). In these rootstocks, increased hydraulic conductivity of fine roots correlates with higher leaf area and transpiration rate in the scion (Gambetta et al. 2012).

Lovisolo and colleagues compared the effect of water stress on rootstocks derived from hybridization of *V. berlandieri* with *V. rupestris* and *V. riparia* (Lovisolo et al. 2008b). They found significant differences in whole-plant root system weight and volume, root hydraulic conductance, as well as soil water depletion rate, which were are all increased in *V. rupestris* crossings. They also showed that embolization contributed to reduce root hydraulic conductance in a wide range of proportion (5-75%) across the different rootstock genotypes. Of note, the extent of embolization was higher in *V. riparia* crossings and was associated with a lower contribution of aquaporin to root hydraulic conductivity (Figure 2). These observations support the hypothesis that the aquaporin-improved root water transport in common rootstock crossings is likely due to the presence *V. rupestris* in their genotypic background.

The intensity of water stress has an impact on the response of drought-resistant rootstocks. Mild stress induces the up-regulation of several aquaporins in 110R roots (Galmes et al. 2007) probably aiming at increasing water absorption capacity to maintain plant activities (vigour induction). In contrast, during severe stress no up-regulation of aquaporins occurs in root cells as long as a re-watering event occurs. This observation is in line with improved hydraulic conductance of drought-resistant grapevine species during mild water deficit and to the phenomenon of recovery from embolism after re-watering, which implies aquaporin expression and solutes redistribution from parenchymal cells to xylem lumen (Brodersen et al. 2010).

Embolisms repair in grapevine roots has been shown to occur when transpiration is low (Perrone et al. 2012b). A proposed mechanism for embolism repair involves a flush of ABA

from the root to the leaf upon re-watering in order to maintain low transpiration and allow the xylem water columns to reform (Lovisolo et al. 2008a; Chitarra et al. 2014). In addition, ABA could directly facilitate aquaporin expression both in roots and in parenchymal cells along the xylem to help this process, as suggested for other plant species (Tyerman et al. 2002; Chaumont et al. 2014). A recent study further extended this relationship to the effect of soil texture and water holding capacity by showing that clay-rich soils induce higher ABA concentrations in leaves which is associated with lower embolism occurrence during moderate water-stress (Tramontini et al. 2014).

Overall, the root response to drought is deeply influenced by the soil properties and the genotype. Several mechanisms are involved in grapevine tolerance to decreasing water availability: they include the production of higher root volumes to reach deeper soil layers and a higher aquaporin expression to improve the root system hydraulic conductivity and reduce the level of embolization. The enhanced water availability obtained by drought-tolerant genotypes in water shortage phases results in greater vigour of the aerial portion of the plant compared to drought-susceptible genotypes.

Rootstock-scion interaction

Water stress induces complex physiological regulation both at the level of root and shoot (especially leaves) in grapevines. The interrelationship between scions and rootstocks in different soils is thus difficult to predict and the sequence of the mechanisms involved in stomatal closure remains to be fully elucidated.

A scion grafted on a drought-resistant rootstock (1103P) shows along the season higher stomatal conductance to water, carbon assimilation rate and evapotranspiration compared to the same scion grafted on drought-susceptible rootstocks (101-14Mgt) (Alsina et al. 2011). This effect on stomatal conductance was associated with Ψ_{leaf} values higher in 1103P than in 101-14Mgt early in the season (June) and lower in the later period (September). This suggests that different rootstock-scion combinations may account for the discrepancy regarding the near-iso/anisohydric behaviours of certain cultivars (Schultz 2003; Vandeleur et al. 2009) that have been varying among different studies (Coupel-Ledru et al. 2014; Martorell et al. 2015). Quantitative trait locus (QTL) analysis have shown that certain rootstock gene loci were associated with scion transpiration, each accounting for less than 10% of the phenotypic variance observed in grafted grapevines (Marguerit et al. 2012). Furthermore, rootstock gene loci involved in scion transpiration rate *per se* differed from loci involved in scion acclimated transpiration rate to water stress. Importantly, the water use efficiency of scion was entirely

correlated to rootstock genetic variability and the loci associated with regulation of scion transpiration rate included many genes linked to aquaporin expression and ABA synthesis or signalling (Marguerit et al. 2012).

A recent study evaluated the effect of grafting different cultivars on either a drought-resistant (140Ru) or a drought-sensitive (SO4) rootstock genotype on stomatal regulation (Tramontini et al. 2013b). The results suggest that rootstocks can modify the scion's stomatal sensitivity to water stress by shifting the level of stomatal closure towards lower (140Ru) or upper (SO4) Ψ_{leaf} independently of the scion's near-iso- or near-anisohydric behaviour. In the same study, a major difference was observed between the intrinsic stomatal response of detached leaf to dehydration and the whole plant response to progressive water deficit. This, once again, stresses the fact that water relations are organ-specific, and that roots may have an important impact on them.

The direct effect of soil, rootstock and scion on the whole-plant tolerance to drought is rather difficult to differentiate and probably depends on complex mechanisms functioning through forward and feedback responses (Vandeleur et al. 2014). Hence, there is a need for gathering the current knowledge on the different scion/rootstock couples in an attempt to highlight the dominant determinants of adaption to drought.

What appears clear from Tramontini and coworkers studies (2013a, b and 2014) is that sandy soils amplify differences in stomatal regulation among cultivars while clayey soils buffer the extremes. Sandy soils, while lowering faster the water resources for the roots, favour the expression of short-term reactions of the plant through stomatal control. In these conditions, the differences among ecophysiological behaviours result particularly evident. On the contrary, clay-rich water-retaining soil, thanks to its shrinking and swelling capacity and by keeping a smaller degree of saturation than a rigid soil, preserves better the water resources and favours a tighter stomatal control, reducing the differences between iso and anisohydric behaviours. Such soil, inducing a mild water stress similar to that obtained with a PRD irrigation scheduling, favours the release of non-hydraulic signals, putatively ABA (Correia et al. 1995; Dodd 2007), without impairing water potential in the plant, but by buffering stomatal function upon water scarcity.

Consequences on berry ripening and quality

The soil effect has been reported to be predominant over genetic characteristics of the grapevine cultivar, so far as to influence the root-to-shoot drought messages (Tramontini et al. 2013a), but it remains to be determined whether it is reflected on the productive potential

of the plants, expressed in terms of yield and quality. The relation between soil-related drought and ABA concentration in roots and shoots (either sap-transported or synthesized in leaf) is well documented, however only a few studies have linked ABA and ABA-glucose ester (GE) concentrations in berries with soil and plant water status; among them, Balint and Reynolds (2013) recently evidenced a high correlation between plant water status and ABA concentration in the berries at harvest.

Yet it is known that grape ripening, independently of plant water status, is an ABA-controlled process, sharing many of the plant responses to water stress inducing phenolic secondary metabolite accumulation in berries (Ferrandino and Lovisolo 2014; Kuhn et al. 2014). As stress conditions imply the accumulation of reactive oxygen species such as hydrogen peroxide, hydroxyl radicals, superoxide, etc., grapevines activate the production of antioxidant molecules, among which secondary metabolites. The control of the biosynthesis of plant phenolics involves overlapping regulatory signals. These include developmental signals and environmental signals for protection against abiotic and biotic stresses. For some of the key compounds, such as flavonoids, there is a deep understanding of the nature of those signals and how the signal transduction pathway connects through the activation of the phenolic biosynthetic genes (Cheynier et al. 2013). However, for many other secondary metabolites, such as volatiles and carotenoids very little is known. It has recently been shown that in leaves of grapevines 'Pinot noir' under severe drought stress many secondary metabolites, belonging to the group of polyphenols as well as volatile compounds, accumulate in higher concentration with respect to non-stressed leaves (Griesser et al. 2015). It remains to be determined whether similar processes are involved in berries and if ABA is one of the triggering mediators.

In *Vitis vinifera* berries, the onset of ripening is tied to sugar accumulation (Gambetta et al. 2010) and it is accompanied by a marked increase in ABA concentration (Deluc et al. 2009). Softening, decreases in turgor, and increases in ABA represent some of the earliest events during the onset of ripening. Later, physical growth, further increases in ABA, and the accumulation of sugars are integral for colour development (Castellarin et al. 2016). However, during berry ripening many other secondary metabolites accumulate, essentially in skins such as other polyphenols, volatiles and carotenoids, etc.

Interestingly the response of *Vitis vinifera* to water stress conditions as to carotenoid accumulation was shown to be dependent on the soil characteristics: in a high water retention capacity soil no difference in the accumulation of carotenoids was detected among vines undergoing different water regimes, whereas in a low water retention capacity soil, berry

carotenoid accumulation was higher in plants suffering from a severe water stress (Oliveira et al., 2003). As carotenoid degradation brings to ABA and norisoprenoid accumulation, as well as to a number of intermediate molecules involved in other lateral biosynthesis pathways such as that of terpenes, deeper knowledge about the effects of soil characteristics on berry quality through ABA mediation is now of primary importance. In addition, the indirect influence of soil properties on berry composition should be considered since it could be mediated via effects on grapevine attributes including canopy, crop and berry sizes (Zerihun et al. 2015).

As a general trend, the highest phenolic concentrations (anthocyanins, in particular) in berries are found in soils with higher clay and/or organic matter content (Choné et al. 2001; Tesic et al. 2001; Morlat and Bodin 2006; Ramos et al. 2015). In addition, a clay-induced soil effect is often greater in wet and intermediate years than in dry years when abundant ABA biosynthesis controls plant responses to drought, independently from soil properties. Notably, the clay-related ABA effects, favourable to grape quality, could be mimicked in vineyards managed with the PRD irrigation mode (Chaves et al. 2010), a consolidated technique addressing ABA effects to both transpiration and grape ripening, independently from soil water-holding capacity.

Final consideration

Taking together the above described plant responses either at the root, shoot, or fruit level, it is possible to intuit that soil (and *terroir*) characteristics be interpreted differently according to the grapevine genotype, and thus have different impacts on transpirative responses. A soil-related influence on ABA synthesis (and catabolism) is pivotal in this response, especially but not only during drought periods, affecting both vegetative growth and fruit ripening.

In detail, anisohydric varieties seem to depend on long-term adaptability mechanisms, ably reflecting differences in type of soil. Isohydric varieties, due to their shorter-term reactions to climatic conditions, could be more able to express the specific characteristics of the year in terms of climate, imposing to the final product the so-called vintage identity. This observation is perhaps premature, but it could set up the objectives for further investigations.

Literature

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Table 1.

Common rootstocks and their drought tolerance level, according to Bavaresco and Lovisolo (2000), Bettiga (2003), Serra et al. (2014), YalumbaNursery©, Nuriootpa, SA 5355, Australia.

Rootstock name	Genotype crossings	Level of tolerance to drought
Riparia Gloire de Montpellier	*V. riparia*	Low: *V. riparia* is highly represented in the east part of north America and has evolved in well exposed and well-watered conditions such as river banks.
Rupestris du lot	*V. Rupestris*	High: *V. Rupestris* originates from central south United-States and has typically evolved in well-exposed and well-drained environments such as rocky to gravelly creek beds.
V. berlandieri	Sometimes referred to as a subspecies of *V. cinerea*	High: *V. berlandieri* originates from central south United-States. It is poorly adapted to grafting but highly resistant to limestone.
101-14Mgt (Millardet et de Grasset)	*V. riparia* × *V. rupestris*	Low
1103 P (Paulsen)	*V. rupestris* ×*V. berlandieri*	High
161-49C	*V. riparia* ×*V. berlandieri*	Low
216-3C	*V. rupestris* ×*V. solonis*	Low
41B (Millardet et de Grasset)	*V. Vinifera* ×*V. berlandieri*	Medium
420A (Millardet et de Grasset)	*V. riparia* ×*V. berlandieri*	Low-medium
3309C (Couderc)	*V. riparia* ×*V. rupestris*	Low-medium
K51-40	*V. rupestris* ×*V. champinii*	Low
Kober 5BB	*V. riparia* ×*V. berlandieri*	Low
Ramsey	*V. champinii*	Medium-high
110 R (Richter)	*V. rupestris* ×*V. berlandieri*	High
140 Ru (Ruggeri)	*V. rupestris* ×*V. berlandieri*	High
Schawrzmann	*V. riparia* ×*V. rupestris*	Medium
SO4 (Selection Oppenhiem)	*V. riparia* ×*V. berlandieri*	Low-medium
Teleki 5C	*V. riparia* ×*V. berlandieri*	Low

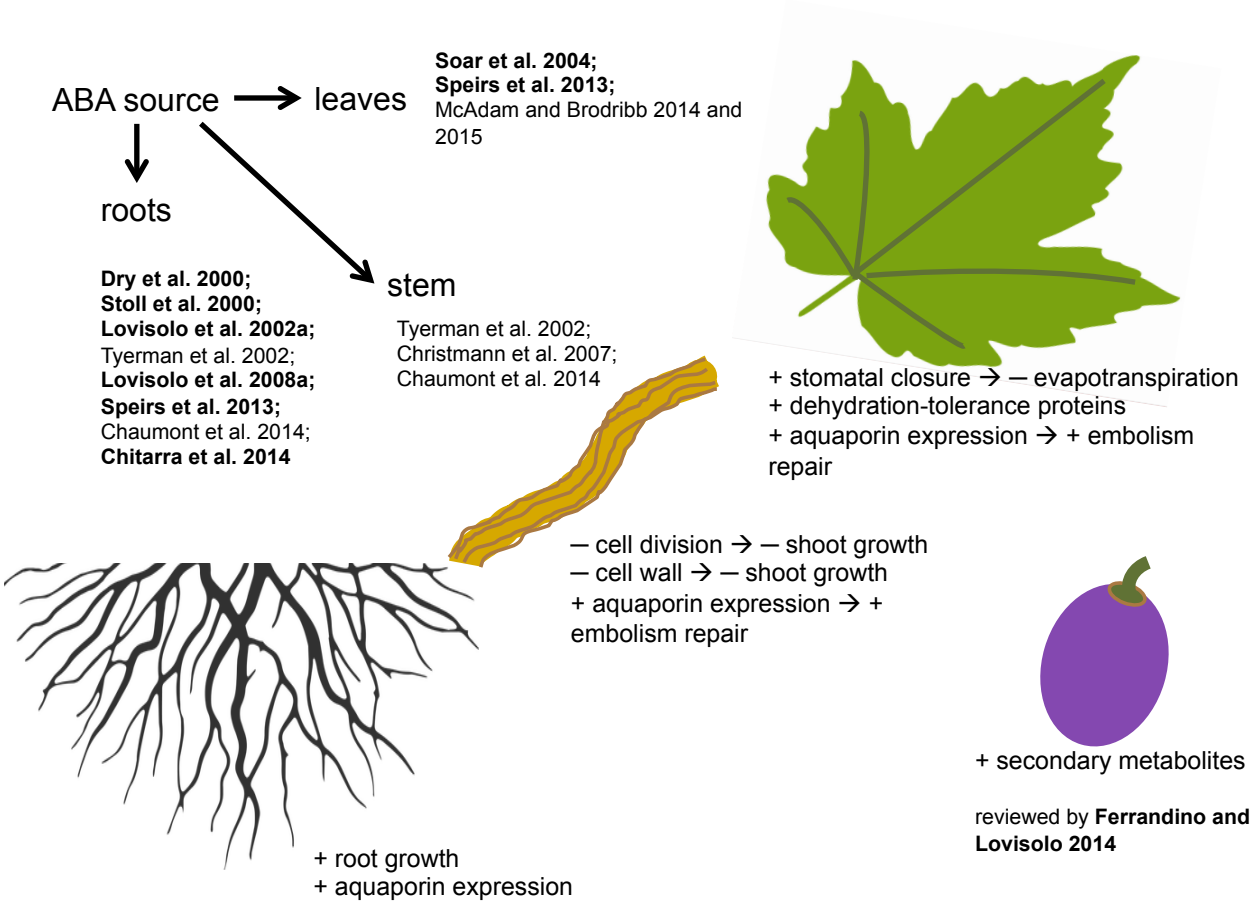

Figure 1.

The left side of the figure provides the evidence supporting theories on localization of ABA synthesis in the plant (listed references are bolded for works conducted on *Vitis* sp.).

The right side of the figure summarizes the main ABA actions in the plant compartments.

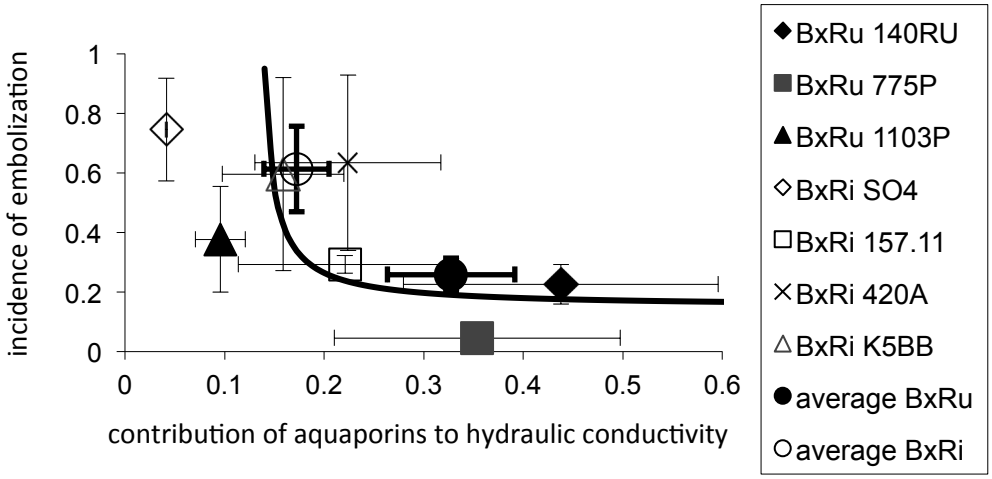

Figure 2.

Interrelationship between the incidence of drought-induced embolization and the contribution of aquaporins to hydraulic conductivity in different crossings of either *V. berlandieri* with *V. rupestris* (BxRu) or *V. riparia* (BxRi). The incidence of vessel embolization was determined by comparing maximal conductance of the roots, which is determined by flushing out xylem embolisms with a pressure of 80KPa, and initial conductance (Lovisolo and Tramontini 2010). The contribution of transmembrane aquaporin-mediated water transport to hydraulic conductivity of the whole root was determined by comparing the proportion of reduced hydraulic conductance of roots perfused with a mercuric chloride solution used to block aquaporin function to maximal root hydraulic conductance.

By using mercuric chloride as inhibitor of cell membrane metabolism (Lovisolo and Schubert 2006) on rootstocks, it was found that the fraction of root water transport under aquaporin-mediated metabolic control is higher in *Vitis rupestris* hybrids: these rootstocks showed lower vessel embolization during water stress (redrawn after Lovisolo et al. 2008b).